LEAF HISTOLOGY AND ITS CONTRIBUTION TO RELATIONSHIPS IN THE MYRTALES[1]

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ABSTRACT

An examination of the leaf histology of a wide array of families thought at one time to be included in the Myrtales has led to a restricted circumscription of the order as follows: Lythraceae, Rhynchocalycaceae, Trapaceae, Oliniaceae, Combretaceae, Alzateaceae, Penaeaceae, Melastomataceae, Crypteroniaceae, Psiloxylaceae, Myrtaceae, and Onagraceae. Data used in testing this concept were obtained from lamina transsections cut to include the midrib. Observations on midrib shape, venation configuration, shape and extent of extraxylary fibers, sclereids, dermal and mesophyll features were most discriminating when examining taxa with the most elaborate and/or generalized anatomy. While leaf histological trends of specialization are not independently producible from this data, correlation with information from leaf architecture should eventually make this possible. Seldom recorded features which have proven useful in this systematic context include length/width ratios of palisade cells and the shape of the boundary between the mesophyll and the midrib ground tissue. The sharpness of tissue differentiation also appears often to be a family characteristic.

In most respects, plant families comprising the core of the Myrtales form a coherent group and the recognition of the order has not been particularly controversial (Dahlgren & Thorne, 1984). At the same time, many of the included taxa pose problems as to their level of recognition as well as to which higher taxon they should be assigned within the order. In addition, more than 30 other families have been assigned to the Myrtales at some time in the recent past (Dahlgren & Thorne, 1984) demonstrating insufficient knowledge of the boundaries of the order as well as its evolutionary background.

A review of the general literature on the circumscription of the order and the evidence used in its definition has been ably dealt with in the other papers from this symposium from the standpoint of general systematic review (Dahlgren & Thorne, 1984; Johnson & Briggs, 1984), wood anatomy (van Vliet & Baas, 1984), leaf architecture (Hickey, 1981), pollen (Patel et al., 1984), and sieve element plastids (Behnke, 1984). I will restrict my comments to the contribution to be made by leaf histology, recognizing that a clear understanding will depend upon a synthesis of all of the above plus data yet to be obtained.

Some formidable problems must be faced when one attempts to use features from young vegetative anatomy in a systematic investigation. First is the insufficient number of studies of this sort

to provide any reliable trends of specialization. I am convinced, however, that leaf histology contains not only valuable diagnostic characters, but that these characters will eventually demonstrate great utility in evolutionary studies. Much of the value will be based on both an increasing number of systematic studies of leaf histology, as well as character correlation with studies of leaf architecture (cf. Hickey, 1981). Leaf structure studies of both types should continue to accumulate rapidly. Leaves are obviously the most easily obtained of all plant materials both from the field and from herbarium collections. While leaves respond readily to evolutionary pressures toward xeromorphy or other modifications, their endomorphic characters commonly retain the ground plan of the phylad to which they belong (Keating, 1984; Dickison, 1970).

In this study a particular problem concerns the interpretation of the data from my sample. The sample appears comprehensive in that 176 species were examined representing 55 genera from 19 families. Actually, the specimens at hand amount to a very small sample of many of the families. Even though attempts were made to choose specimens representing geographic and taxonomic diversity within each family, obviously the family samples most likely do not include the total spectrum of characters to be found in them. The absence of a character from one group does not

TABLE 1. Selected histological features of leaf transections of families of Myrtales.

Taxon	Structure — Dorsiventral	Isobilateral	Trichomes — Simple 1-celled	Simple >1-celled	Complex	Cuticle — Thin	Medium	Thick	Smooth	Ornamented	Epidermis — Adaxial = Abaxial	Adaxial > Abaxial	Adaxial 2× > Abaxial	Adaxial Cells Enlarged	Stomata — Level	Sunken	Adaxial Only	Abaxial Only	Adaxial & Abaxial	Hypoderm	Chlorenchyma — # Palisade Layers	Palisade % Lamina	Length/Width Ratio	# Spongy Layers
LYTHRACEAE																								
Ammannia coccinia	+					+			+		+			+	+				+		1	50	6:1	3
Cuphea spectabilis	+					+			+			+			+				+		1	30	5:1	5
Heimia salicifolia	+					+				+		+			+						1	50	4:1	3
Lafoensia speciosa	+					+			+			+			+			+			1	25	5:1	8
Lagerstroemia speciosa	+					+			+			≥			+			+			2	45	5:1	5
Lawsonia inermis	+					+			+		+				+			+			1(–2)	40	6:1	5
Lythrum alatum var. *lanceolatum*	+					+			+		+				+				+		1(–2)	50	5:1	3
Nesaea longipes	+							+	+		+			+	+				+		1	30	5–6:1	5
Punica granatum	+					+			+			±				+					2	50	4:1	3
Punica protopunica	+			+					+			+			+			+			2(–3)	40	5–8:1	5
Duabanga moluccana	+					+			+			+	+		+			+			2(–3)	50	5–6:1	4
D. grandiflora	+						+		+			+	+		±						2	50	5:1	4
D. grandiflora	+						+		+			+			±			+			2(–3)	50	5–6:1	9
D. moluccana	+					+			+			+			+			+			2	50	4–5:1	4
Sonneratia sp.	+	±						+	+	+						+			+		3–4	30	4:1	11
S. apetala		+						+	+	+						+			+		3 + 3	60	3–4:1	6
RYNCHOCALYCACEAE																								
Rhynchocalyx lawsonioïdes	+					+			+			+			+				+	+	2	60	4:1	5
TRAPACEAE																								
Trapa sp.	+					+			+		±				+			+			2	50	4:1	8
OLINIACEAE																								
Olinia emarginata	+						+	+	+		±				+				+	±	2–3	50	8:1	8

TABLE 1. Continued.

	Structure		Trichomes			Cuticle					Epidermis				Stomata						Chlorenchyma			
	Dorsiventral	Isobilateral	Simple 1-celled	Simple >1-celled	Complex	Thin	Medium	Thick	Smooth	Ornamented	Adaxial = Abaxial	Adaxial > Abaxial	Adaxial 2× > Abaxial	Adaxial Cells Enlarged	Level	Sunken	Adaxial Only	Abaxial Only	Adaxial & Abaxial	Hypoderm	# Palisade Layers	Palisade % Lamina	Length/Width Ratio	# Spongy Layers
COMBRETACEAE																								
Anogeissus leiocarpus		+	+			+		+			+				+			±			1 + 1	50	6:1	3
Buchenavia capitata	+						+	+				+	±		+						1	30	15:1	7
Bucida buceras	+						+	+				+			+			+			1	50	5–10:1	5
Combretum grandiflorum	+						+	+				+			+			+			1	50	8–10:1	5
Conocarpus erectus	±	±					+	+			+			+	+				+	+	3 + 2	50	4:1	5
Guiera senegalensis	+		+		±		+	+				+				±		+			2	50	8:1	5
Lumnitzera racemosa		+					+	+			+				+				+		2 + 2	40	8:1	8
Quisqualis indica	+		+			+		+			+				+			+			1	30	3:1	3
Strephonema pseudocola	+						+	+			+				+			+			1	25	12–15:1	9
Terminalia sp.	+						+		+		+				+			+			1	45	15–20:1	7
ALZATEACEAE																								
Alzatea verticillata	+						+	+	+	±	+				+			+		+	2	25	6:1	20
PENAEACEAE																								
Endonema lateriflora	+						+	+	±			+			+			+			2	30	8:1	8
Penaea mucronata	+						+	+	±		+				+			+			1	45	10:1	5
MELASTOMATACEAE																								
Tibouchina semidecandra	+			+	+			+			+				+			+			1	60	10–12:1	4
Heterocentron subtriplinervum	+			+	+			+					+	+	+			+			1	30	4:1	6
Memecylon blakeoïdes	+						+		+				+	+	+			+			1(–2)	40	2–3:1	3
M. guineense	+						+	+				+			+			+			2	15	1–2:1	4
M. parviflorum	+							+	+	+				+	+			+		±	3–4	40	2–4:1	8

TABLE 1. Continued.

	Histological Features																							
	Structure		Trichomes			Cuticle					Epidermis				Stomata					Chlorenchyma				
	Dorsiventral	Isobilateral	Simple 1-celled	Simple >1-celled	Complex	Thin	Medium	Thick	Smooth	Ornamented	Adaxial = Abaxial	Adaxial > Abaxial	Adaxial 2× > Abaxial	Adaxial Cells Enlarged	Level	Sunken	Adaxial Only	Abaxial Only	Adaxial & Abaxial	Hypoderm	# Palisade Layers	Palisade % Lamina	Length/Width Ratio	# Spongy Layers
M. afzelii	+							+	+			+			+			+			1	15	5:1	12
M. aylmeri	+			+				+	+				+		+			+			1	10	1–5:1	8
M. lateriflorum	+							+	+				+	+	+			+			1	10	4:1	12
M. sp.	+							+	+				+	+	+			+			2	20	2–3:1	7
Mouriri sp.		±						+	+	±	+				+			+		+	4 + 2	90	5:1	4
M. myrtilloïdes	+							+	+		+				+			+			2	30	1–2:1	4
CRYPTERONIACEAE																								
Axinandra zeylanica	+						+	+			+				+			+			1	10	2:1	9
Crypteronia paniculata	+			+			+	+	+		+				+			+			1(–2)	30	3:1	9
PSILOXYLACEAE																								
Psiloxylon mauritianum	+							+	+		+				+			+			1	20	12:1	15
MYRTACEAE																								
Tristania laurina	+							+	+		+				+			+			2	25	8:1	13
T. conferta	+							+	+	+	+				+			+	+		1	25	12:1	8
Eucalyptus micranthra		+						+		+	+				+				+		3 + 3	80	6:1	3
Syzygium paniculatum	+			+				+						+	+			+			2	40	6:1	7
Acmena smithii	+							+	+		+				+			+			1–2	15	12:1	11
Heteropyxis sp.	+						+	+					+		+			+			1	45	8–10:1	4
ONAGRACEAE	+	+	+				+				+	+			+			+	+		1–2	15–25	2–5:1	3–7

preclude a relationship between the two groups being compared. In spite of this, samples of many families demonstrate unique combinations of characters which will be commented on, often as negating relationships between taxa. The available anatomical literature on each family was consulted in order to record the known structural variability.

MATERIALS AND METHODS

All specimens available for this study were liquid preserved in either FAA or FPA at 50% alcoholic strength. Collection data follows each family description and vouchers are maintained at MO unless otherwise noted. Leaf specimens were removed for sectioning from the midrib and the margin, approximately equidistant between the lamina base and apex. The specimens were paraffin-embedded and sectioned at 10 μm on a rotary microtome (Sass, 1958). Most preparations were stained in Safranin-O, Fast Green FCF.

After a preliminary survey of the genera, the features discussed below (cf. Table 1) were selected for thorough observation. Studies by Dickison (1970), Böcher (1979), Pyykkö (1966), and Dahlgren (1968) were useful guides for initial selection of characters. Numerous other useful characters exist which should be included when individual families are studied intensively. Each of those finally selected was found to be diagnostic or systematically stable even though the evolutionary trends of specialization are as yet unknown for most of them.

Lamina structure: Dorsiventral or isobilateral.
Midrib: Shape or profile for the adaxial and abaxial surfaces. Also noted is the degree of abruptness or discreteness of the lamina as it joins the midrib. In all illustrations, adaxial is uppermost and all descriptive data are taken from that orientation.
Midvein and secondary veins: Shape or course in transsection. Presence and configuration of internal or intraxylary phloem. This is often described in relation to extraxylary fibers.
Extraxylary or periphloic fibers: These often affect the shape of the vein, especially secondary veins which may be transcurrent or round, etc., on the basis of the shape of fiber patches or sheaths.
Epidermis: Features include relative thicknesses of the adaxial and abaxial layers whether the surfaces are level or the cells papillose or other unusual shape, whether the cells are enlarged

and/or rounded internally causing the palisade layer to undulate, and whether the cells have gummy, crystalline, or other contents.
Cuticle: Relative thickness, degree of ornamentation and whether the cuticle is flanged between the epidermal anticlinal walls. Normally, the adaxial epidermal cuticle is rated for thickness; the abaxial cuticle is usually thinner except on isobilateral leaves.
Stomata: These are noted as to the surface on which they occur and whether they are level, sunken, or otherwise modified.
Margin: There are a number of marginal shapes and modifications such as the type of marginal vasculature, thickenings, or gland types if present. Insufficient comparable data is at hand for this feature and it is therefore largely not taken into consideration in this report.
Hypodermis: Position and number of layers.
Mesophyll: Chlorenchyma is noted as to number of cell layers of the palisade zone and its percent of the total mesophyll thickness. The length/width ratio of palisade cells is also noted as is the approximate number of spongy layers. These features often appear surprisingly constant for certain families.
Sclereids: Type, position, and wall thickness are recorded.
Secretory cells, ducts: Type and position and presence of epithelium are recorded.
Cellular inclusions: Tannin cells are not usually noted since I have insufficient information as to the age of the specimens and its effect on tannin deposition. Crystal type, size, texture, and position are noted. Crystals are birefringent unless otherwise noted and probably made of calcium oxalate based on shape diagnosis (Franceschi & Horner, 1980; Frey-Wyssling, 1981).

Arrangement of the observations follows the systematic listing of Dahlgren and Thorne (1984). Individual genera are often noted separately if they have been noted in the past as being controversial or anomalous.

OBSERVATIONS

Lythraceae (Figs. 1–8, 10–15)

The genera *Duabanga, Sonneratia,* and *Punica,* often not included in the Lythraceae, are described separately below. In many species, one or both epidermal layers tend to be formed of large, rounded cells. Certain of them are con-
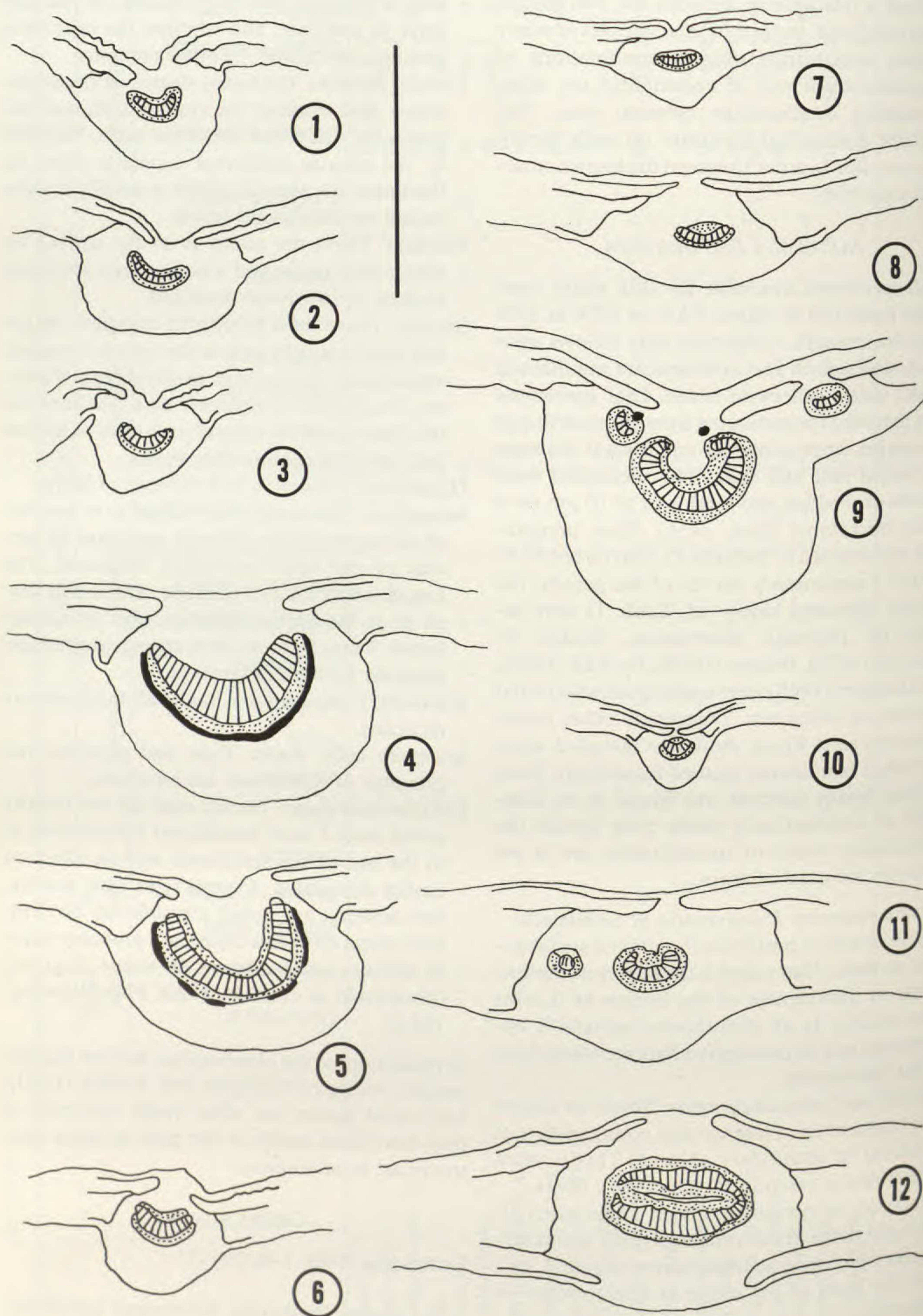
FIGURES 1–12.   Midrib transverse sections of Lythraceae, Sonneratiaceae, and Punicaceae.—1. *Ammannia coccinia.*—2. *Cuphea spectabilis.*—3. *Heimia salicifolia.*—4. *Lagerstroemia speciosa.*—5. *Lafoënsia speciosa.*—6. *Lawsonia inermis.*—7. *Lythrum alatum* var. *lanceolatum.*—8. *Nesaea longipes.*—9. *Rhynchocalyx lawsonioides.*—10. *Punica granatum.*—11. *Sonneratia* sp.—12. *Sonneratia apetala.* Scale line = 1 mm. Legend for all figures: Hatching = xylem, stippling = phloem, solid black = extraxylary fibers.
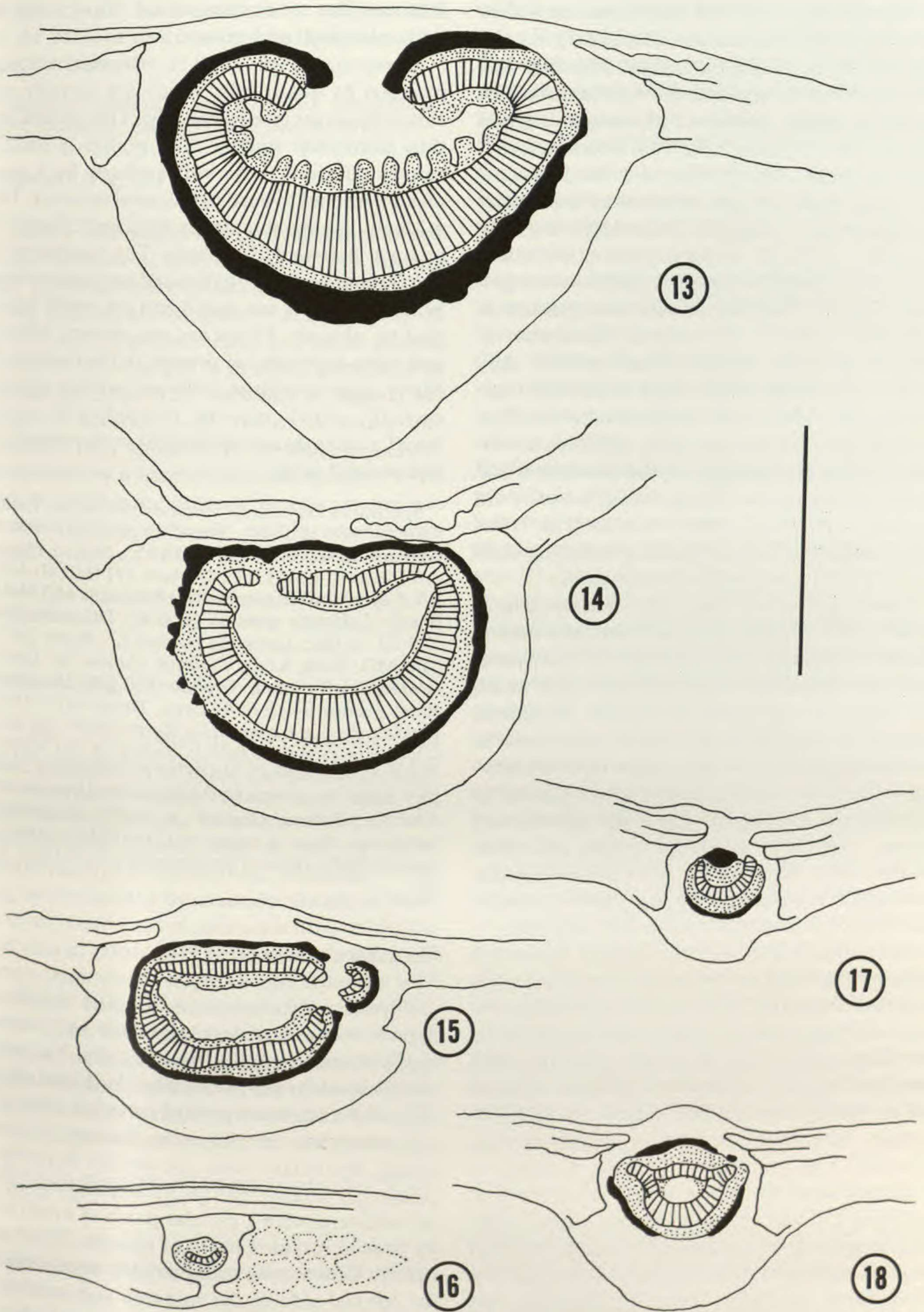
FIGURES 13–18.   Midrib transverse sections of Sonneratiaceae, Trapaceae, Oliniaceae, and Combretaceae.—13. *Duabanga grandiflora.*—14. *Duabanga moluccana.*—15. *Duabanga moluccana.*—16. *Trapa* sp.—17. *Olinia emarginata.*—18. *Terminalia* sp. Scale line = 1 mm.

spicuously larger than the others and may often have mucilaginous contents. The midrib may be grooved, level, or slightly ridged adaxially and often prominently rounded-convex abaxially. The midrib is nearly immersed in *Nesaea longipes* (Fig. 8). The midveins vary from a complete cylinder to deeply semicircular to a fairly shallow arc. Most midveins are bicollateral, but others are apparently collateral. Secondary veins are generally collateral. In most genera, secondary veins are rounded except in *Lagerstroemia speciosa* (Fig. 4) which has an adaxial transcurrent extension formed of parenchyma. Extraxylary fibers are generally absent. When present, they form an abaxial periphloic band on both the midvein and secondary veins [*Lafoënsia speciosa* (Fig. 5) and *Lagerstroemia speciosa*]. Sclereids are absent. Druses are common in the mesophyll and midrib ground tissue. Occasional prismatics are found in *Lafoënsia*. *Lythrum alatum* (Fig. 7) has a few epidermal cells containing radiating clusters of birefringent needle-like crystals.

Punica granatum (Fig. 10). The midrib is slightly and broadly grooved adaxially and is rounded abaxially. The midvein is a bicollateral short arc. Secondary veins are short arcs which are collateral and round in outline. Mesophyll tissue is developed in the midrib quite close to the lateral and adaxial sides of the midvein leaving most of the midrib ground tissue abaxial to the midvein. Extraxylary fibers and sclereids are absent. Very large prismatic crystals and some smaller ones occur in the palisade and spongy mesophyll. A few of the large crystals have central druse-like clusters around their equator.

Duabanga (Figs. 13–15). Adaxial epidermal cells are flattened on the surface but are deeply rounded internally. Some of the larger ones contain mucilage. Abaxial epidermal cells on two of the three species are all deeply papillose with baculum-shaped knobbed extensions, each of which has an ornamented cuticle on its distal surface. The midrib is level or slightly convex adaxially and prominently convex-rounded or V-shaped abaxially. The midvein is a somewhat flattened cylinder with one or two adaxial gaps or a broad crescent shape with deeply incurved adaxial ends. Midveins and secondary veins are bicollateral. Secondary veins are flattened arcs or are circular in different species. Periphloic fibers surround midveins and secondary veins. Some mesophyll cells appear to be lignified but markedly idioblastic sclereids were not found. Druses vary by species from absent to large, coarse

and complex to medium-sized. They occur in mid-mesophyll and around veins.

Sonneratia (Figs. 11, 12). Stomata are surrounded by guard cells which are partially enclosed by larger epidermal cells. The stomata are thus somewhat sunken. The midrib is slightly convex abaxially or on both surfaces. Both samples are or tend toward isobilateral structure. The midvein is a dorsiventrally flattened cylinder or an open flattened "U" shape. The vasculature is bicollateral on the midvein and secondary veins. Secondary veins are round and are nearly encircled by phloem. Fibers are not present. Macro- and astro-sclereids are present in the mesophyll. Many large mucilage cells are present subepidermally which may be of epidermal origin. Small, coarse druses are present in the mesophyll and around veins.

Specimens examined: *Ammannia coccinia* Rottb., *Graham 489* (MICH), Texas; *Cuphea spectabilis* S. Graham, *Reveal et al. 4339* (MARY), Mexico; *Heimia salicifolia* (H.B.K.) Link., *Graham 141* (MICH), Mexico; *Lagerstroemia speciosa* (L.) Pers., cult. MO 74248, Brazil; *Lafoensis speciosa* (H.B.K.) DC., cult. FTG X-5-20, s. loc.; *Lawsonia inermis* L., *Raven 26570*, cult. MO, Hong Kong; *Lythrum alatum* var. *lanceolatum* (Ell.) Rothrock, *Graham 460* (MICH), Mississippi; *Nesaea longipes* A. Gray, *Turner 6163* (TEX), Mexico; *Punica granatum* L., *Raven 26569*, cult. MO, s. loc.; *P. protopunica* Balf. f., *Rudall s.n.* (K), Socotra; *Duabanga grandiflora* (Roxb. ex DC.) Walpers, *Sahni s.n.*, India; *Stone 12837*, Malaya; *D. moluccana* Bl., *Chai s.n.*, Borneo; *Madani s.n.*, 3/5/77, Sadah; *Sonneratia* sp., *Stone & Anderson 13165* (SAN), Sabah; *S. apetala* Buch.-Ham., *Thanikaimoni s.n.*, 3/15/77, India.

Rhynchocalycaceae (Fig. 9)

Rhynchocalyx lawsonioïdes. The midrib is slightly concave or level adaxially and prominently rounded-protruding abaxially. The midvein is semicircular, somewhat V-shaped abaxially with a tendency toward incurved ends with reduced xylem development. Phloem is bicollateral. Secondary veins are similar in configuration only smaller than the midvein. Minor veins are collateral with a circular patch of xylem and an abaxial rounded patch of phloem. Fibers are scanty. One or two small patches are found on the adaxial side of the midvein and secondary veins. Minor veins have a transcurrent adaxial fiber patch which nearly doubles the vein height. Sclereids are absent. Coarse-textured, medium-sized druses are common in midmesophyll and in midrib ground tissue. The large adaxial epi-

dermal cells are flat on the surface and rounded on the palisade side making the palisade zone appear to undulate.

Specimen examined: *Rhynchocalyx lawsonioïdes* Oliv., *Raven s.n.,* cult. MO 7442, South Africa.

Trapaceae (Fig. 16)

Trapa. The midrib is immersed and centered within the zone of aerenchyma of this floating leaf. The small midvein has a rounded patch of xylem with an arc of phloem abaxial to it. A narrow zone of ground tissue (a bundle sheath) surrounds the vein and is in direct proximity to the palisade zone. The vein may be slightly bicollateral. Secondary and minor veins are uncommon. They appear to be bicollateral and are surrounded by a parenchymatous sheath. No fibers or sclereids are present. Druses are present around veins, in palisade, and in aerenchyma zones.

Specimen examined: *Trapa* sp., *Hellquist s.n.* 6/77, Massachusetts.

Oliniaceae (Fig. 17)

Olinia. The midrib is level adaxially and slightly rounded abaxially. The midvein is semicircular and bicollateral. Secondary veins are collateral or bicollateral. Periphloic fibers form a well-developed abaxial band as well as a deep adaxial patch over the midvein. Secondary veins may be surrounded by a circular sheath of fibers or by an interrupted sheath consisting of abaxial and adaxial portions. The adaxial portion may form a transcurrent ridge. Diffuse sclereids were not noted. Large or medium-sized, coarse-textured druses are found mostly near veins with some in mid-mesophyll. A large, dense mass of druses was found abaxial to the midvein fibers. The leaf margin is slightly recurved and consists of a multiple-layered hypoderm-like tissue.

Specimen examined: *Olinia emarginata* Burtt-Davy, *Goldblatt 1466* (MO) cult. Kirstenbosch, South Africa.

Combretaceae (including *Strephonema*) (Figs. 18–27)

The midrib is often conspicuously circular in outline. Lamina sectors commonly insert laterally leaving a well-formed adaxial ridge. *Combretum* (Fig. 24) and *Quisqualis* (Fig. 23) have a

midrib protruding prominently on the abaxial side. The midvein is commonly cylindrical or a flattened cylinder. A pair of gaps are often present opposite the lamina insertion. *Combretum* has a three-quarter cylinder open adaxially. *Quisqualis* and *Conocarpus* (Fig. 25) have semicircular or broad arc midveins. The midveins appear collateral with weak development of bicollateral phloem in some specimens. Secondary and tertiary veins are quite variable and possibly diagnostic. While some are circular, most tend to be transcurrent with parenchymatous sheath extensions. *Buchenavia* (Fig. 20) and *Terminalia* (Fig. 18) have fiber sheaths with extensions forming transcurrent veins. Other genera have fibers in sheaths, adaxial-abaxial patches, or in scanty patterns. Fibers also surround midveins. In *Buchenavia,* adaxial fibers form sheaths around prominent discrete patches of adaxial phloem. Sclereids are not common. In *Bucida* (Fig. 21), fibrous sclereids are well developed under the adaxial epidermis and attach to veins at transcurrent extensions. Some occur isolated in the palisade region. *Buchenavia* also has vein extensions where fibers occasionally develop away from the extensions. *Strephonema* (Fig. 27) has macrosclereids and trichosclereids common in the lamina in any orientation. Very large druses are common in enlarged cells of the mesophyll in all genera examined and some have styloid projections. A few prismatics are found in *Strephonema.*

Lumnitzera racemosa (Fig. 22). The cuticle is thick, smooth, and flanged over thickened outer periclinal walls on both adaxial and abaxial epidermal layers. Outer palisade layers beneath both surfaces have dense, red-staining contents. The midrib is nearly immersed but the abaxial side shows a slight convex curvature. The midvein is a broad arc with collateral phloem. Fibers and sclereids are absent. Medium-sized, coarse druses are common and randomly placed in the mesophyll.

Specimens examined: *Anogeissus leiocarpus* (DC.) Guill. & Perr., *Pilz 2088,* Nigeria; *Buchenavia capitata* (Vahl.) Eichler, *Raven 26623,* cult. MO, s. loc.; *Bucida buceras* L., *Raven 26618,* cult. MO, Puerto Rico; *Combretum grandiflorum* G. Don, cult. FTG X-2-328, s. loc.; *Conocarpus erectus* L., *Raven 26619,* cult. MO, Puerto Rico; *Guiera senegalensis* Lam., *Sreemadhavan 5800,* Nigeria; *Lumnitzera racemosa* Willd., cult. FTG 64-4585, s. loc.; *Quisqualis indica* L., *Raven 26572,* cult. MO, s. loc.; *Strephonema pseudocola* A. Chev., *Hall & Nabooh 46647,* Ghana; *Terminalia* sp., cult. FTG X-2-2700, s. loc.
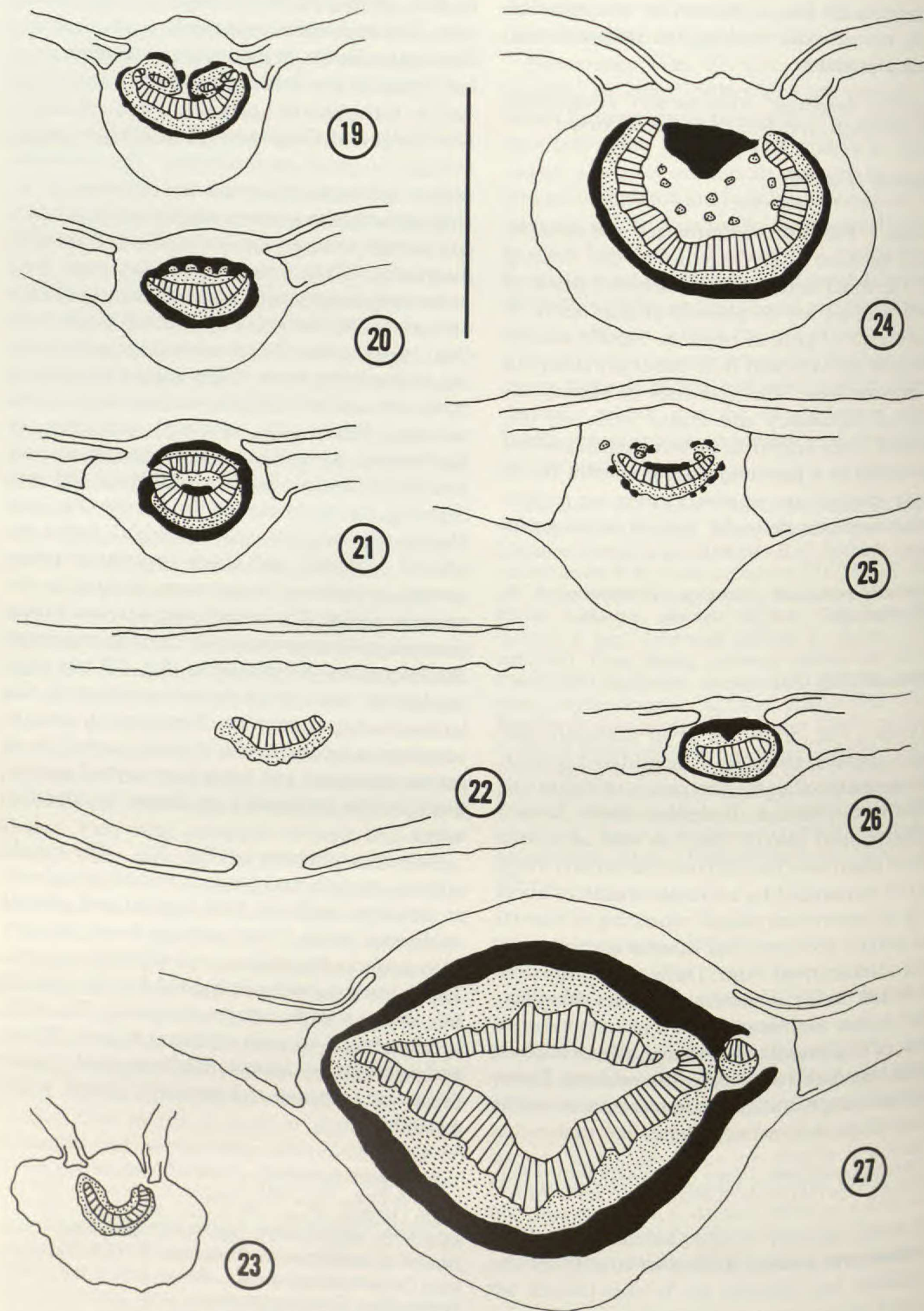
FIGURES 19–27.   Midrib transverse sections of Combretaceae.—19. *Anogeissus leiocarpus.*—20. *Buchenavia capitata.*—21. *Bucida buceras.*—22. *Lumnitzera racemosa.*—23. *Quisqualis indica.*—24. *Combretum grandiflorum.*—25. *Conocarpus erectus.*—26. *Guiera senegalensis.*—27. *Strephonema pseudocola.* Scale line = 1 mm.
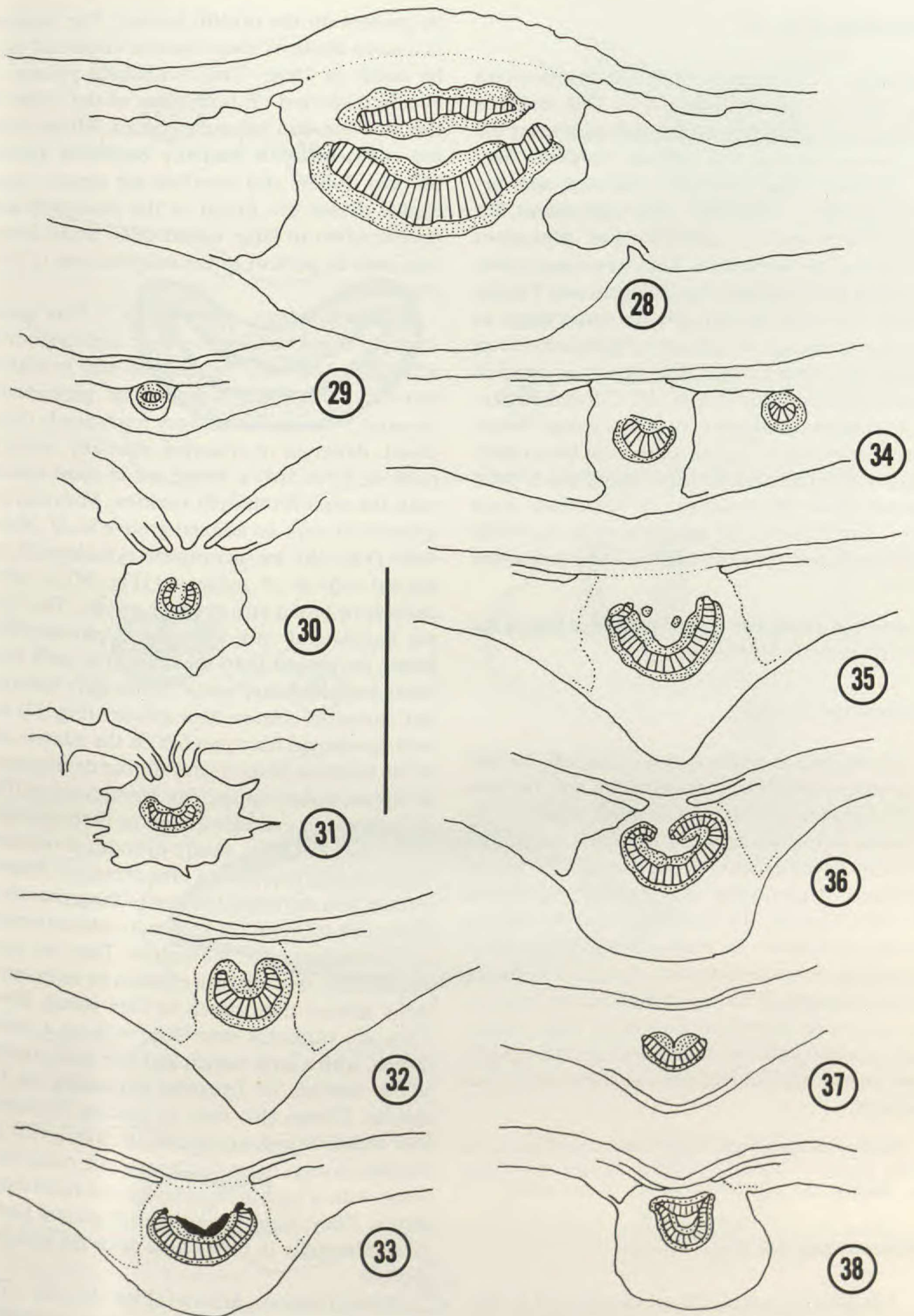
FIGURES 28–38.   Midrib transverse sections of Alzateaceae, Penaeaceae, and Melastomataceae.—28. *Alzatea verticillata.*—29. *Penaea mucronata.*—30. *Heterocentron subtriplinervum.*—31. *Tibouchina semidecandra.*—32. *Memecylon afzelii.*—33. *Memecylon aylmeri.*—34. *Memecylon parviflorum.*—35. *Memecylon lateriflorum.*—36. *Memecylon guineense.*—37. *Memecylon oligoneurum.*—38. *Memecylon blakeoïdes.* Scale line = 1 mm.

Alzateaceae (Fig. 28)

Alzatea. The midrib is moderately convex on both surfaces and not prominent. The midvein is a flattened cylinder with lacunae separating the bicollateral adaxial and abaxial portions. Secondary and minor veins are collateral and circular in outline. Extraxylary fibers are absent, but large, thin-walled sclereids are abundant throughout the mesophyll. They have been called branched foliar sclereids by Dahlgren and Thorne (1984). The cells are actually the same shape as the armed spongy or palisade chlorenchyma in which they appear and they occur as lignified single cells or groups of cells. A 1–2 layered adaxial hypoderm is present over the lamina which may become up to 7 layers deep over the midrib. Baas (1979) reported that the hypoderm is present only over the midrib in *A. verticillata* from Peru. Small druses are uncommon in the lower mesophyll and near the midvein and secondary veins.

Specimen examined: *Alzatea verticillata* Ruiz & Pavón, *Poveda s.n.,* Costa Rica.

Penaeaceae (Fig. 29)

The midrib is small, convex abaxially in *Endonema,* or totally immersed in *Penaea.* The partially bicollateral midvein is small, round to elliptical, and with a short arc of xylem. Adaxially, phloem development is restricted to the lateral portions of the xylem. Sclereids are fibrous in *Penaea,* beneath the epidermis and at random in the mesophyll. In *Endonema,* the abundant branched astrosclereids with elongated arms are found throughout the mesophyll but are concentrated in mid-mesophyll. Druses are large, coarse, and complex and are found beneath the epidermis on the adaxial and abaxial sides of the mesophyll.

Specimens examined: *Endonema lateriflora* (L. f.) Gilg, *Rourke 1706,* South Africa; *Penaea mucronata* L., *Barker 332,* cult. Kirstenbosch, South Africa.
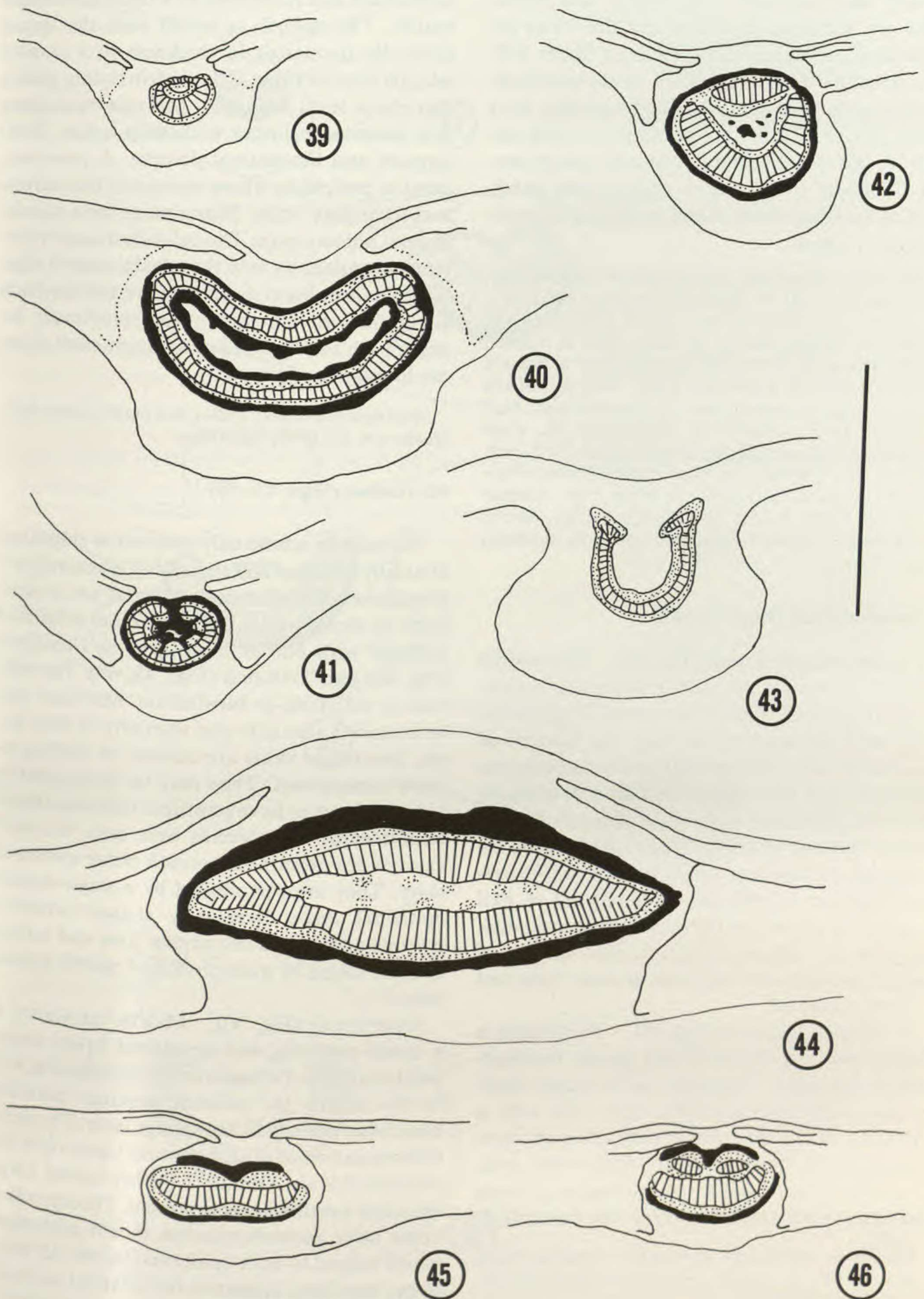
Melastomataceae (Figs. 30–41)

Adaxial epidermal cells are exceptional in *Heterocentron* (Fig. 30) in being large, flat on the surface and irregular and rounded on the palisade side. The midrib is large and rounded with lamina sectors inserted near the top of the adaxial side. Large, pyramidal, multicellular hairs may be present on the midrib surface. The midvein is a semi-circle or three-quarter circle and may be small or large. The bicollateral phloem is evenly dispersed on both sides of the xylem of the midvein and secondary veins. Minor veins are collateral with partially encircling abaxial phloem. Fibers and sclereids are absent. Large coarse druses are found in the mesophyll and midrib often in large round cells. Small druses may also be present in the midvein area of *Heterocentron.*

Memecyloideae, Memecylon. This genus forms midribs which are level or slightly grooved adaxially. Abaxially the midribs may be slightly convex, somewhat V-shaped or prominently rounded. The midveins vary from nearly cylindrical, flattened or rounded adaxially, semicircular or form only a broad arc in those species with the least prominent midribs. Midveins are cylindrical with an adaxial groove in *M. blakeoïdes* (Fig. 38), an incomplete cylinder with incurved ends in *M. guineense* (Fig. 36), or semicircular or broad arcs in other species. The veins are bicollateral with the adaxial phloem often better developed than the abaxial in both midveins and secondary veins. Extraxylary fibers are not common. *Memecylon aylmeri* (Fig. 33) has well-developed fiber patches on the adaxial side of the midvein phloem and similar development on the secondary veins. The *Memecylon* sp. (Fig. 41) has a fiber cylinder bounding both outer and inner phloem of its nearly cylindrical midvein. The secondary veins are also encircled. Phloem is often best developed closest to the protoxylem. Fiber-like sclereids are common subepidermally and throughout the mesophyll. They are commonly dispersed without relation to veins but in some species they attach to vein sheath fibers. They are variously seen to be without a visible lumen, with a large lumen and thin walls, rounded in outline, or irregular depending on the species. Druses also vary by species. Prismatics and coarse druses are found in *Memecylon* sp. Smaller druses, more finely textured, occur as do some with a hollow-appearing non-birefringent center. They occur in the midrib ground tissue, subepidermally in the lamina or in the mid-mesophyll.

Memecyloideae, Mouriri (Figs. 39, 40). The midrib is grooved adaxially and is protruding and somewhat flattened abaxially. Midvein xylem is a flattened cylinder surrounded by phloem externally and internally. Large midveins have periphloic fibers forming a thin sheath both ex-

FIGURES 39–46. Midrib transverse sections of Melastomataceae, Crypteroniaceae, Psiloxylaceae, and Myrtaceae.—39. *Mouriri myrtilloïdes.*—40. *Mouriri* sp.—41. *Memecylon* sp.—42. *Crypteronia paniculata.*—43. *Axinandra zeylanica.*—44. *Psiloxylon mauritianum.*—45. *Acmena smithii.*—46. *Eucalyptus micrantha.* Scale line = 1 mm.

ternally and internally. Secondary and minor veins are sheathed by fibers and the veins are bicollateral. Smaller leaves have no fibers. Diffuse sclereids are common in mid-mesophyll. They may be branched or armed and may have a large lumen. Druses are common in mid-mesophyll and are medium-sized and coarse-textured. Phloem of secondary veins is best developed on the adaxial side. Abaxial phloem is poorly formed or absent.

Specimens examined: *Heterocentron subtriplinervum* (Link & Otto) A. Braun & Bouche, cult. LA, s. loc.; *Memecylon afzelii* G. Don, *Hall & Nabooh 46601,* Ghana; *M. aylmeri* Hutch. & Dalz., *Hall & Nabooh 46632,* Ghana; *M. blakeoïdes* G. Don, *Hall & Nabooh 46628,* Ghana; *M. guineense* Keay, *Hall & Nabooh 46629,* Ghana; *M. lateriflorum* (G. Don) Bremek., *Hall & Nabooh 46630,* Ghana; *M. oligoneurum* Bl., *Chai s.n.,* Borneo; *M. parviflorum* Thw., *Leiden 2978,* cult. Bogor, s. loc.; *Mouriri myrtilloïdes* (Sw.) Poiret, *Wurdack & Wurdack 2624,* Jamaica; *Mouriri* sp., *Madani s.n.* 5/3/77 (SAN 81060), Sabah; *Mouriri* sp., *Gentry 18524,* Peru; *Tibouchina semidecandra* (Schr. & Mart.) Cogn., *Raven 26571,* cult. MO, s. loc.

Crypteroniaceae (Figs. 42, 43)

Crypteronia paniculata (Fig. 42). The midrib is nearly level adaxially and prominently rounded-protruding abaxially. The overall shape is circular with lamina inserted near the summit of the adaxial side. The midvein is circular with the xylem divided into abaxial and adaxial portions which are separated by lacunae opposite the position of lamina insertion. The vasculature is bicollateral. Extraxylary fibers form a well-developed cylinder around the outer phloem as well as scattered patches in the center of the midvein. Sclereids are absent. Medium-sized druses, of medium texture, are common around veins and in mid-mesophyll.

Axinandra zeylanica (Fig. 43). The midrib is slightly grooved adaxially and deeply rounded-convex abaxially. The midvein is deeply semicircular with small incurved ends. The vein is uniformly bicollateral. Secondary veins are short collateral arcs. No sclereids or fibers were seen. Prismatic crystals appear in midrib ground tissue and many small druses occur in the mesophyll.

Specimens examined: *Axinandra zeylanica* Thw., *Faden 76/466,* Sri Lanka; *Crypteronia paniculata* Bl., *Stone 13280,* Thailand.

Psiloxylaceae (Fig. 44)

Psiloxylon mauritianum. The thick adaxial epidermis has paradermal thickenings beneath the surface and is covered by a thick non-flanged cuticle. The midrib is broad with the lamina gradually increasing in thickness to a rounded adaxial convex ridge. The midrib is only slightly convex or level abaxially. Midvein vasculature is a flattened cylinder with deep xylem development and bicollateral phloem. A prominent band of periphloic fibers surrounds the midvein and secondary veins. Minor veins have adaxial-abaxial phloem caps. The palisade mesophyll extends prominently into the adaxial midrib ridge. Sclereids are absent. Secretory cavities lined with an epithelium are present subepidermally beneath both surfaces. A few medium-sized druses are found near veins.

Specimen examined: *Psiloxylon mauritianum* Baill., *Gueho s.n.* 12/1976, Mauritius.

Myrtaceae (Figs. 45–50)

The midrib is adaxially grooved or ridged and abaxially rounded and the midrib is generally not prominent. The midvein is a broad arc or semicircle in most species but approaches a flattened cylinder with one or more gaps in *Eucalyptus* (Fig. 46) and *Tristania* (Figs. 48, 49). The midvein is collateral or bicollateral. Midveins may be bounded adaxially and abaxially by fiber layers. Secondary veins are circular or tending toward transcurrent. They may be surrounded by a ring of fibers or have prominent adaxial-abaxial bundle caps. No sclereids were seen. Secretory cavities are prominent beneath either epidermal layer. They are surrounded by a single distinct epithelial layer. Irregularly shaped prismatic crystals and druses of varying sizes and texture may be found in mesophyll and midrib ground tissue.

Heteropyxis (Fig. 50). Midrib vasculature is a broad arc with well-developed xylem somewhat similar to *Tristania* and *Syzygium* (Fig. 47). In the midrib, the palisade impinges adaxially somewhat more than the spongy layer. The sharp differentiation of midrib ground tissue from the mesophyll is also similar to the Myrtaceae. Large secretory cavities are also present. The secondary veins have parenchymatous sheath extensions which extend to both epidermal layers. All veins in my specimen appear to be collateral although they are reported to be bicollateral by Schmid (1980). Sclereids and periphloic fibers are absent.

Specimens examined: *Acmena smithii* (Poir.) Merrill & Perry, *Schmid 1968-A2,* cult. LAM, Australia; *Eucalyptus micrantha* DC., *Schmid 1969-A3,* cult LAM,
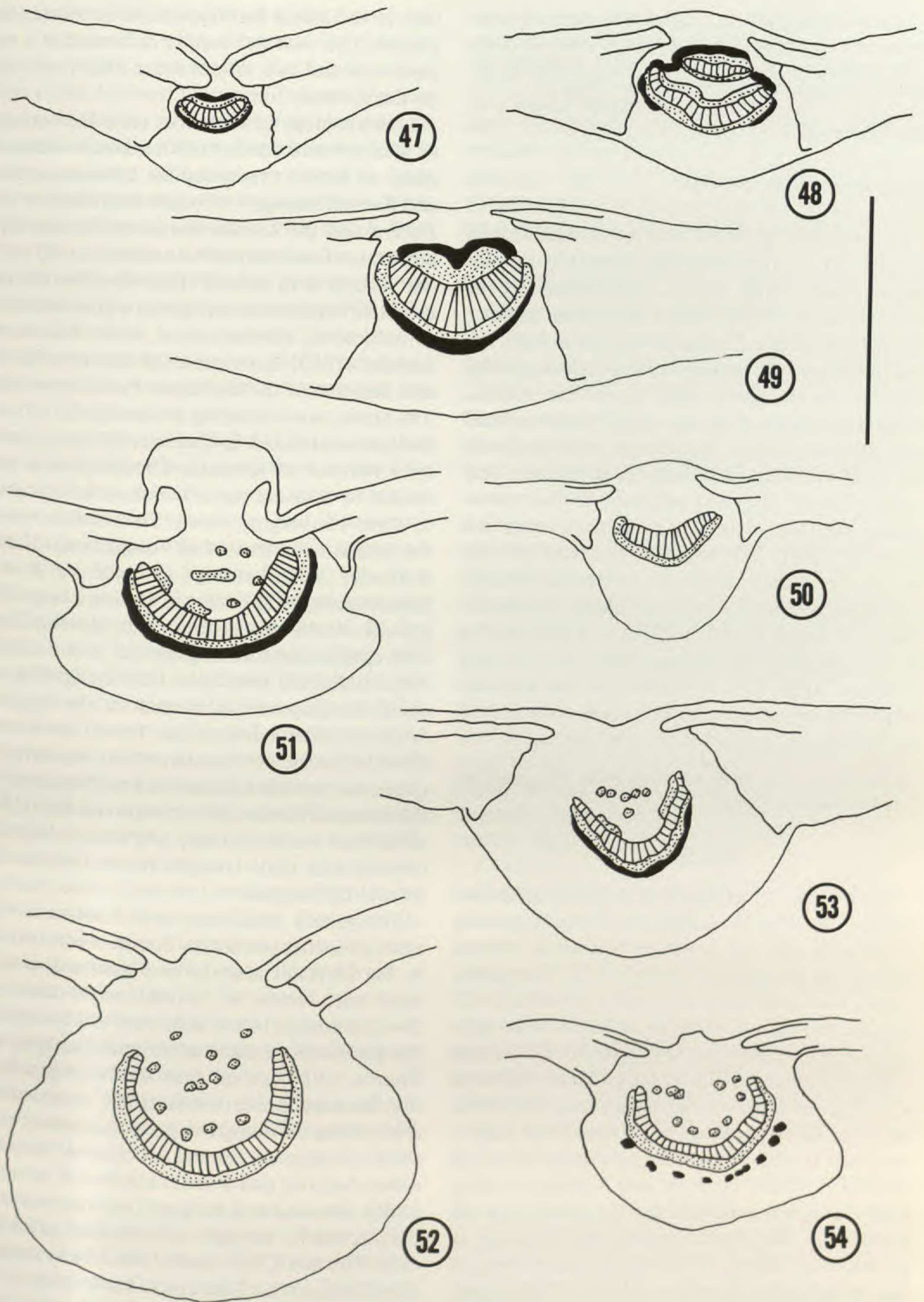
FIGURES 47–54.   Midrib transverse sections of Myrtaceae and Onagraceae.—47. *Syzygium paniculatum.*—48. *Tristania conferta.*—49. *Tristania laurina.*—50. *Heteropyxis* sp.—51. *Ludwigia peruviana.*—52. *Fuchsia boliviana.*—53. *Hauya heydeana.*—54. *Hauya elegans.* Scale line = 1 mm.

Australia; *Heteropyxis* sp., cult. LAM, South Africa; *Syzigium paniculatum* Gaertn., *Schmid 1969-A1*, cult. LAM, Australia; *Syzigium* sp., *Faden 76/438B*, Sri Lanka; *Tristania conferta* R. Brown, *Ching s.n.*, 2/77, cult. LAM, s. loc.; *T. laurina* R. Brown, *Hagen s.n.*, cult. Lam, s. loc.

Onagraceae (Figs. 51–54)

The midrib is grooved or ridged adaxially and prominently convex-rounded abaxially in the largest dorsiventral leaves. Isobilateral leaves often have a midrib which protrudes equally above both surfaces. Midribs may be sharply demarcated from the lamina or may show a gradual decrease in thickness away from the midrib. Midveins vary from deeply semicircular to small arcs. Phloem may be bicollateral at the midvein but often the adaxial phloem is not closely and symmetrically disposed adjacent to the protoxylem but instead occurs as patches separated from the xylem. The smallest midveins are collateral. Secondary veins are generally circular, collateral, and always without fibers. Periphloic fibers are noted in the midribs in a few species of *Fuchsia* (Fig. 52), *Hauya* (Figs. 53, 54), and *Ludwigia* (Fig. 51). Sclereids are not present. Raphides are present in all genera with druses and prismatics restricted to a few genera.

Specimens examined: 125 species in 17 genera as listed in Keating (1982).

Discussion

Lythraceae. Leaf anatomy is made quite heterogeneous with the addition of *Duabanga* and *Sonneratia* and the family is held to be a basal one in the Myrtales (Thorne, 1976; Cronquist, 1981). One specimen of *Lagerstoemia* has the largest midvein, a complete cylinder with substantial periphloic fiber development. Epidermal cells are characteristically irregular in thickness with frequent large, rounded, mucilage-filled cells. Baas and Zweypfenning (1979) stated that *Lagerstroemia* is unambiguously advanced in wood characters while Graham and Graham (1971) held that it was primitive for the family. On the hypothesis that more complex leaf histology is primitive in leaves of Myrtales, *Lagerstroemia* has to be judged primitive. Bailey (1951), however, stated clearly that different organs of the plant may evolve structurally at different rates.

Ross and Suessenguth (1926) reported nine out of ten American *Lafoënsia* spp. have leaves with a hydathodal tip. The tip is very similar in structure to the apical leaf hydathode in *Punica* (see below). The vascular supply is formed of a median vein and two lateral veins which converge on the epithem tissue.

Leaf histology of *Punica* as recorded here and in Metcalfe and Chalk (1950) fits well within the range of features recorded for Lythraceae. Baas and Zweypfenning (1979) noted similarities with *Punica* and the Lythraceae as well as the Myrtaceae. Leaf anatomy offers no objection to merging *Punica* with one of these families but this might be expected of any genus which has leaves as reduced as *Punica*'s seem to be. Turner and Lersten (1983) have reported on the structure and function of the leaf tip in *Punica granatum.* The acute, mucronate tip is hydathodal with the foramen connected to the external environment by a number of stomata. The foramen is subtended by epithem tissue which, in turn, is distal to three converging veins. The median vein is the largest as is true of all rosoid teeth (Hickey & Wolfe, 1975). Leaf tips in *Lafoënsia* (Ross & Suessenguth, 1926) differ in having a large schizenous or schizolysigenous cavity develop, lined with epithem and leading directly to the outside. Also, *Lafoënsia* may have heavily lignified tracheid development proximal to the epithem. Aside from these differences, Turner and Lersten (1983) note the obvious structural similarity between the families Lythraceae and Punicaceae on this complex feature. Bridgewater and Baas (1978) noted that wood anatomy of *Punica* is also specialized and that it shares derived status with several Lythraceae.

The genera *Duabanga* and *Sonneratia* have among the most strikingly complex leaf anatomy in the Myrtales and the two genera also differ from each other in several ways. Baas and Zweypfenning (1979) noted the distinctness of the genera from each other and Dahlgren and Thorne (1984) stated that the homogeneity of the Sonneratiaceae needs to be reconsidered. *Sonneratia*, the mangrove genus, has leaves which show tendencies toward isobilateral development. Adaxial and abaxial epidermal layers are nearly identical and the guard cells are markedly overarched by strongly cuticularized subsidiary cells. Rao and Chakraborti (1982) have reported on the structure of the apical knob of the emarginate leaf of *Sonneratia caseolaris* (L.) Engl. This leaf has a highly dentritic, flared, vascularized "pad" with veins ending in club-like aggregations of brachytracheoids. An epithem seems to be present, but the authors report finding no outlet

to the surface. This apical knob is not rosoid nor does it seem to have any structural homologies with other teeth reported for the family. *Duabanga* of the lowland forests of Indomalaya has dorsiventral leaves with either a thicker adaxial epidermis or with an abaxial epidermis which is strongly papillate. Sclereids are found in both genera which also serve to separate them from Lythraceae (Bannerjee & Rao, 1975; Rao & Das, 1979). The question of whether the two genera are sufficiently closely related to be placed in the same subfamily is not easily answered. While the two are distinctive in my sample, there is considerable anatomical variation within each genus which must be assessed before venturing an opinion. Leaf venation architecture would be especially instructive here. Muller (1981) noted that the pollen of *Florschuetzia trilobata* of the Oligocene and Miocene of Borneo seems to combine characteristics of Lythraceae and Sonneratiaceae, supporting the hypothesis of a common evolutionary history. Venkateswarlu and Rao (1964) concluded on the basis of wood anatomy that *Duabanga* and *Sonneratia* should be included in the Lythraceae although Baas and Zweypfenning (1979) noted that this would certainly extend the range of features in that family. If we follow Thorne (1976) and add the two genera to the Lythraceae, they would certainly need their own subfamily or subfamilies.

Rhynchocalycaceae. *Rhynchocalyx lawsonioïdes* with its enlarged adaxial epidermis, midrib and midvein configuration, semi-transcurrent secondary veins, type and position of druses fits well within the Lythraceae. Most characteristic is the extension of palisade tissue from the lamina into the midrib, adaxial to the midvein, a pattern shown by nearly all leaves of Lythraceae. In short, the anatomy of *Rhynchocalyx* in no way extends the anatomical variation in leaf anatomy found in the Lythraceae.

Trapaceae. Leaf anatomy of *Trapa* reflects the specialized floating habit of the genus. The dorsiventral leaves have well-developed aerenchyma in the abaxial two-thirds of the lamina and stomata are on the adaxial surface only. Metcalfe and Chalk (1950) included *Trapa* in the Onagraceae and Airy-Shaw (1973) considered it a close relative of the Onagraceae. Takhtajan (1980) states that Trapaceae is related to the Onagraceae, especially to the genus *Ludwigia*. The leaves of the more generalized species of *Ludwigia* (Keating, 1982) show no resemblance to *Trapa* leaf anatomy. Even those *Ludwigia* species

with floating leaves have not converged on the structure of *Trapa* leaves. The absence of raphides and its unusual histology distinguishes *Trapa* from Onagraceae and Lythraceae but leaves open the question of whether it might be closely related to them in spite of its ecological specializations. The thin, monarch root anatomy of *Trapa* (Fahn, 1974) is probably unique in the Myrtales. Evidence linking *Trapa* with any other family will not likely come from vegetative histological features.

Oliniaceae. Mújica and Cutler (1974) found that leaf anatomy is very useful in *Olinia* for defining intra-generic subgroupings. Rao and Das (1976) and Mújica and Cutler (1974) have noted the presence of terminal sclereids in *Olinia* although these were not observed in my preparations. As figured by Mújica and Cutler, the histological patterns of the leaf midrib and lamina are quite compatible with leaves of Lythraceae and Myrtaceae. Diffuse sclereids are not found. The adaxial patch of fibers at the midvein of *Olinia emarginata* is somewhat similar to the pattern found in *Memecylon aylmeri*. Mújica and Cutler (1974) noted that terminal sclereids similar to those of Oliniaceae occur in species of *Memecylon* and in *Mouriri*. They also noted the similarity of petiole structure in species of *Memecylon* and *Olinia*. Rao and Dahlgren (1968) noted similarities to leaf and wood anatomical features of the Rubiaceae although that family entirely lacks intraxylary phloem.

Combretaceae. In contrast to the work on the leaf epidermis by Stace (1980, and references cited therein), anatomy of the leaf does not produce a clear alignment according to the taxonomic tribes and subtribes of Exell and Stace (1966). The family has generally complex midrib vasculature except in *Conocarpus* which has reduced leaves. *Lumnitzera* and *Laguncularia*, the mangrove genera, also show reduced and specialized anatomy including hydathodes. Striking features of the family are the very large druses and styloid-druse combinations which are formed in large cells often occupying the entire height of the lamina in *Anogeissus*, and to a lesser extent in *Bucida*, *Terminalia*, and *Guiera*. In contrast to the finding of a number of unusual embryological features in *Guiera* by Venkateswarlu and Rao (1972), I found no particularly distinctive vegetative features in that genus. Tobe and Raven's (1983) conclusion, that *Guiera*'s unusual embryological features are of secondary origin, is supported by vegetative anatomy. Overall, the

Combretaceae appear to have a coherent set of leaf anatomical features and one can agree with Dahlgren and Thorne (1984) that no particularly close connection with other families of the order is obvious.

Strephonema seems clearly related to the Combretaceae with its midvein cylinder, and secondary veins with fiber caps. The large, coarse druses and prismatic crystals, fiber-like and macrosclereids, and the characteristic length/width ratio of the palisade cells are all clearly combretaceous. On the other hand, the midvein and secondary vasculature of *Strephonema* seem to be free of intraxylary phloem. This serves to isolate the genus somewhat but all of the Combretaceae I have observed have relatively weak intraxylary phloem development. Anomocytic stomata in *Strephonema* differ from the mostly parasitic members of the Combretaceae and the cyclocytic mangrove genera. Outer and Fundter (1976) felt that phloem, bark and wood characteristics plead for a less specialized and distinct subfamily of Combretaceae. However, the lack of intraxylary phloem would appear to be a secondary loss if that character is regarded as basic for the Myrtales.

Alzateaceae. Few specimens of the genus are known and we probably do not have a good circumscription of its variation. As with the specimen studied here, Baas (1979) noted that his Costa Rican specimen has a hypoderm over all of the mesophyll whereas the Peruvian specimens have a hypoderm extending over the veins only. The isolation from other myrtalean families pointed out by Dahlgren and Thorne (1984) can be confirmed on the basis of leaf histology although the genus does seem clearly to belong to the order. Features which serve to isolate *Alzatea* include the sclereids, which are simply lignified idioblastic cells of the same shape as spongy cells, the cyclocytic combined with anomocytic stomata, the three-trace, trilacunar node, the broken cylinder of midvein vasculature, and the particular form of small square epidermal cells as seen in transection.

The structure of the mesophyll and of the veins is generally similar to several myrtalean families (Crypteroniaceae, Myrtaceae, and Lythraceae) but not a clear fit into any of them. Midrib and lamina structure is quite different from *Rhynchocalyx* and does not support the contention of van Beusekom-Osinga and van Beusekom (1975) that they belong together in a subfamily of Crypteroniaceae. Maintenance of the monogeneric Al-

zateaceae is best supported on the basis of vegetative anatomy.

Penaeaceae. The seven, closely related genera have small coriaceous leaves, often with an ericoid habit (Airy-Shaw, 1973). Midveins and midribs are small and reduced in complexity which precludes useful systematic comparisons with those features. Dahlgren (1968) stated that leaf anatomy does not contribute much to differences between genera of the family. Dahlgren (1968) also noted that the families Geissolomataceae, Oliniaceae, Thymelaeaceae, Melastomataceae, Combretaceae, and Lythraceae have all been considered closely allied on the basis of a variety of features. The array of diffuse and terminal sclereids reported by Rao and Das (1976) as well as the leaf axil bristles serve to isolate the family from all other Myrtales except possibly the Melastomataceae-Memecyloideae. Sclereids of the Memecyloideae recall those of Penaeaceae as does the specialized leaf margin consisting of a parenchymatous ridge as found in both *Memecylon* and *Penaea*. Large, coarse and complex druses are also found in both groups.

Melastomataceae. The family is distinctive morphologically and anatomically. A comprehensive anatomical study of the young vegetative anatomy of the family would doubtless provide a number of diagnostic features and morphoclines (cf. Metcalfe & Chalk, 1950). By far the greatest number of leaf anatomical studies have been done of *Mouriri* and *Memecylon* of the Memecyloideae. These works have demonstrated that sclereids of all types occur in these genera and that they are biogeographically and systematically correlated (Foster, 1947; Subramanyam & Rao, 1949; Morley, 1953; Rao, 1957; Rao & Dakshni, 1963; Rao & Bhupal, 1974; Rao & Jacques-Felix, 1978; Bremmer, 1979; and Rao et al., 1980). Baas (1981) has called attention to the systematically useful stomatal and crystal types in the family. Midrib vasculature in the Melastomatoideae is much more diverse than implied by the sample included here and it should be thoroughly studied. Reduction and simplification of midrib structure in both subfamilies suggest parallel trends of specialization.

An interesting feature noted only in the Memecyloideae involves the configuration of the phloem. In both *Memecylon* and *Mouriri*, the intraxylary phloem of midveins and secondary veins is usually better developed than the abaxial or collateral phloem. In secondary veins, the abaxial phloem is often missing being replaced

with robust development of the adaxial phloem. This tendency is especially pronounced in *Memecylon*. Relationships of the Melastomataceae to other myrtalean families are not readily suggested on the basis of leaf features.

Crypteroniaceae. The delimitation of this family by van Beusekom-Osinga and van Beusekom (1975) included five genera and resulted in a diverse group from the standpoint of leaf histology. In spite of that diversity, van Vliet et al. (1981) included the genera as a subfamily within the Melastomataceae. Removal of *Alzatea* and *Rhynchocalyx* improves the family (or subfamily) circumscription, although *Rhynchocalyx* does retain certain resemblances to *Axinandra*. These include the midrib shape, the midvein shape with the incurved ends of the semicircle. The *Axinandra* specimen examined here is probably somewhat immature and probably will not bear extensive comparison. *Crypteronia paniculata* examined here has more prominent vasculature than most Lythraceae but it has several features similar to that family. The simple trichomes, palisade cell measurement ratios, palisade percentage of the mesophyll, number of spongy layers, and the shape of secondary veins with a convex xylem adjacent to normal collateral phloem are all similar. Among myrtalean families, Lythraceae show the greatest similarities to the Crypteroniaceae even though van Vliet and Baas (1975) found no resemblance on wood features.

Psiloxylaceae. Psiloxylon mauritianum shows sufficiently distinct leaf histology to support the concept of its belonging to a separate family as Dahlgren and Thorne (1984) conclude in their review. The epithelium-lined secretory cavities found in *Psiloxylon* leaves are otherwise rare in the Myrtales except in the Myrtaceae. Midrib and midvein configuration in the genus are unique among reports known to me. On the basis of data from reproductive organs, Briggs and Johnson (1979) state that "a conceivable common ancestor of *Psiloxylon* and the Myrtaceae would be decidedly un-Myrtaceous, in contrast to such an ancestor for the genera included in the family . . . ." The array of leaf features compared in the present study at least confirm that *Psiloxylon* is properly placed in the Myrtales sensu stricto. If broad family concepts are used, *Psiloxylon* would be best assigned to the Myrtaceae as a subfamily as proposed by Schmid (1980). There is insufficient information on the leaf anatomy of many genera of Myrtaceae to

make a judgment on that basis either to include or exclude *Psiloxylon* from the Myrtaceae.

Myrtaceae. Briggs and Johnson (1979; Johnson & Briggs, 1984) have provided a list of characters, including a few leaf histological and architectural features, which may be reasonably inferred to be present in primitive Myrtaceae. The specimens which I examined were mesomorphic, dorsiventral, and lacking a hypoderm, all generalized features by the criteria listed by Briggs and Johnson. As noted by Metcalfe and Chalk (1950), Johnson (1980), and Erdtman and Metcalfe (1963), isobilateral leaves with a hypoderm are common in the family. In leaf midvein vasculature patterns, one might hypothesize a trend of specialization which will have to be tested with much more data. A semicircular-shaped trace may have evolved in two directions: 1) the trace has become reduced to a broad then narrow arc of tissue by simple reduction, and 2) the trace has become incurved adaxially and then flattened as noted in *Eucalyptus obliqua* L'Herit. (Metcalfe & Chalk, 1950) and *Eucalyptus micrantha* (Fig. 46) as illustrated in this study. *Acmena smithii* may represent an extreme form of an arc where adaxial xylem portions have been lost and only the adaxial periphloic fibers remain. The trends noted by Briggs and Johnson (1979) toward microphylly, serial modification, more organized leaf architecture, isobilateral and centric growth, and anomalous secondary venation, suggest that discovery of many trends of vascular and other histological specialization will repay a comprehensive study of the family.

Histological features of *Heteropyxis* leaves, including the midrib vasculature, mesophyll structure, and the presence of the characteristic secretory cavities, are generally compatible with other myrtacean genera. These features plus those in the exhaustive list in Schmid's (1980) review, support the inclusion of the genus within the Myrtaceae.

The family as presently circumscribed does not show obvious affinities with any other families of the order except Psiloxylaceae. The inclusion of Lecythidaceae in the family by Bentham and Hooker (1862) was shown to be unreasonable by Metcalfe and Chalk (1950) and it seems clear that Lecythidaceae should be excluded from the order entirely.

Onagraceae. This family, without doubt the best studied family of its size among the flowering plants, was recently thoroughly examined for its leaf architectural and anatomical features

(Hickey, 1980; Keating, 1982). For leaf histology, 125 species representing all 17 genera were studied and only a brief summary of the conclusions will be repeated here. The family is a natural coherent group and all of the genera share a number of features which also serve to isolate the family within the Myrtales. These include the presence of raphide crystals (Keating, 1982), the four-nucleate (*Oenothera*-type) embryo sac (Tobe & Raven, 1983), and viscin threads on the pollen (Skvarla et al., 1977). The genera of Onagraceae which show the best developed midrib vasculature (*Ludwigia, Fuchsia*, and *Hauya*, as figured here) show a unique arrangement of intraxylary phloem compared to all other myrtalean specimens that I have examined. The traces are not strictly bicollateral but instead the phloem on the adaxial side consists of individual strands in the midvein ground tissue often at some distance from the midvein protoxylem. The adaxial phloem strands are not collectively oriented with respect to the shape of the midvein xylem.

As the evolution of the family is presently understood (cf. Raven, 1979) the leaf anatomy trends of the family represent a reduction series in complexity of structure and developmental sequences. In their general conformation of leaf histology, the Onagraceae show their greatest similarity to the Lythraceae. Punicaceae leaves are also compatible but are too reduced for reliable comparison. Many onagraceous genera have druses and prismatic crystals as well as styloids (especially *Ludwigia* and *Hauya*) which serve to link the family to other myrtalean families. Leaf teeth are highly distinctive having a hydathodal apparatus including an apical foramen, epithem tissue, and three converging veins. Named the "rosoid" tooth by Hickey and Wolfe (1975), it is only known from several saxifragalean genera (Stern, 1974, 1978; Stern et al., 1970; Styer & Stern, 1979a, 1979b), the Onagraceae (Hickey, 1980; Keating, 1982, 1984), the Lythraceae (Hickey, 1981; Ross & Suessenguth, 1926), and the Punicaceae (Turner & Lersten, 1983).

SUMMARY OF CROSS SECTIONAL LEAF HISTOLOGY FEATURES FOR THE ORDER MYRTALES

The following ordinal description is based mostly on the species described above, which have more generalized anatomy. The inclusion of a large sample of more specialized species

would have lengthened this treatment several fold, decreasing its utility.

Leaf structure is mostly dorsiventral with isobilateral leaves occurring in several families. Adaxial and abaxial epidermal cells are of equal thickness or the adaxial cells may be up to 2–3 times as thick as the abaxial. Epidermal cells may be convex or level on the surface or facing the mesophyll, and regular or irregular in shape. Mucilage cells may occur in epidermal cells in the Lythraceae. The cuticle is thick to thin or not visible. A hypoderm layer is rarely present in most families although it is fairly common in the Myrtaceae in genera with isobilateral leaves. The midrib in dorsiventral leaves may be grooved, level, or ridged on the adaxial side. It may be very large and rounded on the abaxial side, ranging to immersed or level. In isobilateral leaves, the midrib may be biconvex or circular, to level or immersed. The lamina may be abruptly differentiated from the midrib or it may taper gradually from a poorly defined midrib. Midveins normally consist of a single trace varying from a deep semicircle to a broad or short arc and are either collateral or bicollateral. Secondary veins are collateral or bicollateral with the phloem on the adaxial side occasionally the best developed. Extraxylary fibers are absent to scarce or well developed when they form abaxial phloem caps or full sheaths. Fibers may form transcurrent extensions over the smaller veins. Sclereids, as astrosclereids, macrosclereids, or trichosclereids, may be absent or rarely present to abundant. The mesophyll may be weakly or sharply differentiated into palisade and spongy layers. The 1–2 palisade layers have cells which vary from $2:1$ to $12:1$ length/width ratios. Spongy mesophyll cells may form a well organized aerenchyma in genera with floating leaves. Stomata are mostly abaxial in dorsiventral leaves but are found on both surfaces on some dorsiventral leaves and on all isobilateral leaves. Calcium oxalate crystals are always present in one or more forms as styloids, prismatics, raphides, druses, or crystal sand. They may be randomly dispersed in the mesophyll, restricted to upper or lower layers of the mesophyll, or occur only around veins. Margins are usually without unusual modifications but occasionally hypoderm or other lignified or collenchymatous, non-mesophyll cells may form a thickened edge. Marginal teeth, when present, are probably always rosoid and have a hydathodal structure. Secretory cavities are rare but

are present and epithelium-lined in some Myrtaceae.

COMMENTS ON FAMILIES OFTEN INCLUDED IN THE MYRTALES

Thymelaeaceae. Leaf anatomical features of the family, minus *Gonystylus* are generally within the range as recorded for the core myrtalean families. Diverse anatomical features include a papillose adaxial epidermis, a characteristic form of fibrous sclereid (Metcalfe & Chalk, 1950), a hypoderm, mucilaginous epidermal cells, and several crystal types including styloids, prismatics, druses, and crystal sand. Margins may be supported by "veins" which are actually sclerenchymatous elements (Metcalfe & Chalk, 1950). About half of the genera are recorded as having bicollateral vascular bundles. In most of my specimens, the midrib is small with an arc of vasculature with two exceptions. A small cylinder is noted in *Lethedon* and *Daphnopsis.*

The remaining genus, *Gonystylus,* is quite exceptional for the family and it is certainly not myrtalean. Its midrib is very large, prominently protruding, and rounded abaxially. The vasculature consists of a broken cylinder in one species, and in the other, a broad cylinder of collateral bundles. The cylinder surrounds an inner U-shaped vein which in turn contains several smaller bundles. Each cycle of traces is capped by well-developed periphloic fibers. *Gonystylus* also contains epithelium-lined mucilage cavities which occur in the palisade region. Cronquist (1981) includes *Gonystylus* in the family while Dahlgren and Thorne (1984) state that evidence suggests that not only is *Gonystylus* questionably included in the family, it may not even be closely allied to it. A thorough study of the anatomy of the family would need to consider the specialized xeromorphic nature of many of the species.

Haloragaceae. Leaves of this family have reduced venation and generally simplified structure. With this data, it is impossible to affirm or deny affinities with practically any order.

Rhizophoraceae. This family fits poorly into the Myrtales on a number of grounds. The cylindrical or incurved arc of midvein vasculature shows a marked tendency to be dissected in many species. The phloem commonly remains a continuous collateral band. A prominent hypoderm is common which may be multilayered. The innermost layer is often comprised of large cells

which extend separately down into the palisade zone in *Rhizophora* and *Gynotroches.* Some of these large cells may extend out to the adaxial epidermal surface. Laticifers, often articulated, are common in some species throughout the spongy and midrib zones. Complex midvein vasculature is present in *Carallia brachiata.* The family needs more anatomical study both for better circumscription and for a better understanding of its characters in light of its mangrove habit. The family is quite variable anatomically.

Lecythidaceae (including Barringtoniaceae). The family is distinctive in midrib shape and vasculature. Most specimens are convex adaxially and abaxially in various combinations of rounded and V-shaped profiles. The lamina sectors are horizontally or laterally inserted. The collateral midrib venation is highly complex. *Lecythis, Gustavia,* and *Couroupita* have one large flattened cylinder toward the adaxial side of the midrib which is encircled abaxially by a series of smaller cortical bundles which often have centrically arranged xylem, i.e., have radial symmetry with encircling phloem. A row of small bundles may also partially surround the main cylinder on the adaxial side. Each genus has a particular diagnostic arrangement of the bundles which in some cases are numerous. The genera *Barringtonia, Careya,* and *Combretodendron,* sometimes recognized as the Barringtoniaceae (Airy-Shaw, 1973) are distinguished as a group although they are comparable in complexity and clearly related to the Lecythidaceae sensu stricto. Those genera have an abaxially placed, deep U-shaped trace or flattened cylinder with an array of wing bundles pointing toward the laterally inserted lamina sectors. Adaxial or abaxial rows of accessory veins may be present. The palisade mesophyll extends into the midrib zone beneath nearly the entire adaxial surface but is not continuous across the midrib. Trichomes, when present, have a multicellular buttressed base of complex and characteristic form.

The closest pattern of midrib vasculature to this highly distinctive family appears to be among the Theales near the Guttiferae, Ochnaceae, Quiinaceae, and Theaceae as figured by Schofield (1968). The overall configuration of Lecythidaceae leaf histology is strikingly similar to those families.

Chrysobalanaceae. Species examined here all have cylindrical midvein vasculature with prominent midribs. *Parinari nonda* shows the most

complex midrib venation described with xylem and phloem bands enclosed within the main vascular cylinder. Venation is collateral. What appears to be internal phloem in some species may be due to loss of part of the included vasculature. The genera examined could fit into Myrtales in terms of the configuration of characters present.

Elaeagnaceae. The peltate and multicellular stalked hairs are not matched by any other myrtalean families. Midveins and midrib configuration are compatible with the order but bicollateral phloem is absent. The raphides recorded throughout the leaf of *Elaeagnus philippinensis* are rare in the Myrtales. The Onagraceae, the only other family with raphides, otherwise shares few characters with the Elaeagnaceae.

Elatinaceae. Young vegatative features seem to exclude this family from the Myrtales, even when discounting obvious specializations for aquatic habitats. Nodal anatomy with split lateral traces, the presence of leaf lamina traces which were never fused with the midvein, leaf primordia fused to sheathing stipules at the nodal level, stalked glandular trichomes on the young stem, and strictly collateral vascular bundles form a combination of characters not found within the order.

LITERATURE CITED

AIRY-SHAW, H. K. 1973. J. C. Willis' A Dictionary of the Flowering Plants and Ferns, 8th edition. Cambridge Univ. Press, Cambridge.

BAAS, P. 1979. The anatomy of *Alzatea* Ruiz & Pav. (Myrtales). Acta Bot. Neerl. 28: 156–158.

———. 1981. A note on stomatal types and crystals in the leaves of Melastomataceae. Blumea 27: 475–479.

——— & R. C. V. J. ZWEYPFENNING. 1979. Wood anatomy of the Lythraceae. Acta Bot. Neerl. 28: 117–155.

BAILEY, I. W. 1951. The use and abuse of anatomical data in the study of phylogeny and classification. Phytomorphology 1: 67–79.

BANNERJEE, B. C. & T. A. RAO. 1975. On foliar sclereids in a few species of *Sonneratia*. Curr. Sci. 44: 639–640.

BEHNKE, H.-D. 1984 [1985]. Ultrastructure of sieve-element plastids of Myrtales and allied groups. Ann. Missouri Bot. Gard. 71: 824–831.

BENTHAM, G. & J. D. HOOKER. 1862. Genera Plantarum. Reeve & Co., London.

BEUSEKOM-OSINGA, R. J. VAN & C. F. VAN BEUSEKOM. 1975. Delimitation and subdivision of the Crypteroniaceae (Myrtales). Blumea 22: 255–266.

BÖCHER, T. W. 1979. Xeromorphic leaf types. Evolutionary strategies and tentative semophyletic sequences. Kongel. Danske Vidensk. Selsk. Biol. Skr. 22(8): 1–71.

BREMMER, K. 1979. Taxonomy of *Memecylon* (Melastomataceae) in Ceylon. Opera Bot. 50: 1–32.

BRIDGEWATER, S. D. & P. BAAS. 1978. Wood anatomy of the Punicaceae. IAWA Bull. 1978/1: 3–6.

BRIGGS, B. G. & L. A. S. JOHNSON. 1979. Evolution in the Myrtaceae—evidence from inflorescence structure. Proc. Linn. Soc. New South Wales 102(4): 157–256.

CRONQUIST, A. 1981. An Integrated System of Classification of Flowering Plants. Columbia Univ. Press, New York.

DAHLGREN, R. 1968. Studies on Penaeaceae II. The genera *Brachysiphon, Sonderothamnus* and *Saltera*. Opera Bot. 18: 1–72.

——— & R. F. THORNE. 1984 [1985]. The order Myrtales: circumscription, variation, and relationships. Ann. Missouri Bot. Gard. 71: 633–699.

DICKISON, W. C. 1970. Comparative morphological studies in the Dilleniaceae. V. Leaf anatomy. J. Arnold Arbor. 51: 89–101.

ERDTMAN, G. & C. R. METCALFE. 1963. Affinities of certain genera *incertae sedis* suggested by pollen morphology and vegetative anatomy. I. The myrtaceous affinity of *Kania eugenioides* Schltr. Kew Bull. 17: 249–250; II. The myrtaceous affinity of *Tristania merguensis* Griff. (*Thorelia deglupta* Hance). Kew Bull. 17: 251–252.

EXELL, A. W. & C. A. STACE. 1966. Revision of the Combretaceae. Bol. Soc. Brot., Ser. 2, 40: 5–26.

FAHN, A. 1974. Plant Anatomy, 2nd edition. Pergamon Press, Oxford.

FOSTER, A. S. 1947. Structure and ontogeny of the terminal sclereids in the leaf of *Mouriri huberi* Cogn. Amer. J. Bot. 34: 501–514.

FRANCESCHI, V. R. & H. T. HORNER, JR. 1980. Calcium oxalate crystals in plants. Bot. Rev. (Lancaster) 46: 361–425.

FREY-WYSSLING, A. 1981. Crystallography of the two hydrates of crystalline calcium oxalate in plants. Amer. J. Bot. 68: 130–141.

GRAHAM, A. & S. A. GRAHAM. 1971. The geologic history of the Lythraceae. Brittonia 23: 335–346.

HICKEY, L. J. 1980. Leaf architecture of Onagraceae. 2nd Int. Cong. Syst. Evol. Biol. Abstracts, p. 69.

———. 1981. Leaf architecture of the Myrtales. 13th Int. Bot. Cong. Sydney, Austral. Abstracts, p. 131.

——— & J. A. WOLFE. 1975. The bases of angiosperm phylogeny: vegetative morphology. Ann. Missouri Bot. Gard. 62: 538–589.

JOHNSON, C. T. 1980. The leaf anatomy of *Leptospermum* Forst. (Myrtaceae). Austral. J. Bot. 28: 77–104.

JOHNSON, L. A. S. & B. G. BRIGGS. 1984 [1985]. Myrtales and Myrtaceae—a phylogenetic analysis. Ann. Missouri Bot. Gard. 71: 700–756.

KEATING, R. C. 1982 [1983]. The evolution and systematics of Onagraceae: leaf anatomy. Ann. Missouri Bot. Gard. 69: 770–803.

———. 1984. Leaf anatomy of *Fuchsia* sect. *Jimenezia* (Onagraceae) from the flora of Panama. In W. G. D'Arcy (editor), Historia Naturelle de Panama. Missouri Bot. Gard., St. Louis (in press).

METCALFE, C. R. & L. CHALK. 1950. Anatomy of the Dicotyledons, 2 Volumes. Oxford Univ. Press, Oxford.

MORLEY, T. 1953. The genus *Mouriri* (Melastomataceae). A sectional revision based on anatomy and morphology. Univ. Calif. Publ. Bot. 26: 223–312.

MÚJICA, M. B. & D. F. CUTLER. 1974. Taxonomic implications of anatomical studies on the Oliniaceae. Kew Bull. 29: 93–123.

MULLER, J. 1981. Fossil pollen records of extant angiosperms. Bot. Rev. (Lancaster) 47: 1–142.

OUTER, R. W. DEN & J. M. FUNDTER. 1976. The secondary phloem of some Combretaceae and the systematic position of *Strephonema pseudocola* A. Chev. Acta Bot. Neerl. 25: 481–493.

PATEL, V. C., SKVARLA, J. J. & P. H. RAVEN. 1984 [1985]. Pollen characters in relation to delimitation of Myrtales. Ann. Missouri Bot. Gard. 71: 858–969.

PYYKKÖ, M. 1966. Leaf anatomy of East Patagonian xeromorphic plants. Ann. Bot. Fenn. 3: 453–622.

RAO, T. A. 1957. Comparative morphology and ontogeny of foliar sclereids in seed plants I. *Memecylon* L. Phytomorphology 7: 306–330.

—— & O. P. BHUPAL. 1974. The utility of sclereid typology in solving problems of synonymy in a few taxa of the genus *Memecylon* L. Proc. Indian Acad. Sci., Sect. B, 80: 291–300.

—— & S. CHAKRABORTI. 1982. A little looked at attribute of the leaves of *Sonneratia caseolaris* (L.) Engl. Curr. Sci. 51: 303–305.

—— & K. M. M. DAKSHNI. 1963. Systematics of *Memecylon*—a preliminary survey based on the sclereid morphology. Proc. Indian Acad. Sci., Sect. B, 58: 28–35.

—— & S. DAS. 1976. On idioblasts in a few taxa of Penaeaceae. Curr. Sci. 45: 750–752.

—— & ——. 1979. Leaf sclereids—occurrence and distribution in the angiosperms. Bot. Not. 132: 319–324.

—— & H. JACQUES-FELIX. 1978. Les types de sclerites foliaires et la classification des *Memecylon* africains. Adansonia n.s. 18: 59–66.

——, K. BREMER & S. CHAKRABORTI. 1980. Foliar sclereids in Sri Lanka (Ceylonese) species of *Memecylon* (Melastomataceae). Bot. Not. 133: 397–401.

RAO, V. S. & R. DAHLGREN. 1968. Studies on Penaeaceae. V. The vascular anatomy of the flower of *Glischrocolla formosa*. Bot. Not. 121: 259–268.

RAVEN, P. H. 1979. A survey of reproductive biology in Onagraceae. New Zealand J. Bot. 17: 575–593.

ROSS, H. & K. SUESSENGUTH. 1926. Das Apikalorgan der Blätter von *Lafoensia*. Flora 120: 1–18.

SASS, J. 1958. Botanical Microtechnique, 3rd edition. Iowa State Univ. Press, Ames.

SCHMID, R. 1980. Comparative anatomy and morphology of *Psiloxylon* and *Heteropyxis*, and the subfamilial and tribal classification of Myrtaceae. Taxon 29: 559–595.

SCHOFIELD, E. K. 1968. Petiole anatomy of the Guttiferae and related families. Mem. New York Bot. Gard. 18: 1–55.

SKVARLA, J. J., P. H. RAVEN, M. G. CHISSOE & M. SHARP. 1977. An ultrastructural study of viscin threads in Onagraceae pollen. Pollen & Spores 20: 5–143.

STACE, C. A. 1980. The significance of the leaf epidermis in the taxonomy of the Combretaceae. V. The genus *Combretum* subgenus *Cacoucia* in Africa. Bot. J. Linn. Soc. 81: 185–203.

STERN, W. L. 1974. Comparative anatomy and systematics of woody Saxifragaceae. *Escallonia*. Bot. J. Linn. Soc. 68: 1–20.

——. 1978. Comparative anatomy and systematics of woody Saxifragaceae. *Hydrangea*. Bot. J. Linn. Soc. 76: 83–113.

——, E. M. SWEITZER & R. E. PHIPPS. 1970. Comparative anatomy and systematics of woody Saxifragaceae. *Ribes*. Pp. 215–237, *in* N. K. B. Robson, D. F. Cutler & M. Gregory (editors), New Research in Plant Anatomy. Bot. J. Linn. Soc. 63. Suppl. 1. Academic Press, London.

STYER, C. H. & W. L. STERN. 1979a. Comparative anatomy and systematics of woody Saxifragaceae. *Philadelphus*. Bot. J. Linn. Soc. 79: 267–289.

—— & ——. 1979b. Comparative anatomy and systematics of woody Saxifragaceae. *Deutzia*. Bot. J. Linn. Soc. 79: 291–319.

SUBRAMANYAM, K. & T. A. RAO. 1949. Foliar sclereids in some species of *Memecylon* L. Proc. Indian Acad. Sci., Sect. B, 15: 291–298.

TAKHTAJAN, A. 1980. Outline of the classification of the flowering plants (Magnoliophyta). Bot. Rev. (Lancaster) 46: 225–359.

THORNE, R. F. 1976. A phylogenetic classification of the Angiospermae. *In* M. K. Hecht, W. C. Steere & B. Wallace (editors), Evol. Biol. 9: 35–106.

TOBE, H. & P. H. RAVEN. 1983. An embryological analysis of Myrtales: its definition and characteristics. Ann. Missouri Bot. Gard. 70: 71–94.

TURNER, G. W. & N. R. LERSTEN. 1983. Apical foliar nectary of pomegranate (*Punica granatum*: Punicaceae). Amer. J. Bot. 70: 475–480.

VENKATESWARLU, J. & P. S. PRAKASA RAO. 1964. The wood anatomy and taxonomic position of Sonneratiaceae. Curr. Sci. 33: 6–9.

—— & ——. 1972. Embryological studies in some Combretaceae. Bot. Not. 125: 161–179.

VLIET, G. J. C. M. VAN & P. BAAS. 1975. Comparative anatomy of the Crypteroniaceae sensu lato. Blumea 22: 173–195.

—— & ——. 1984 [1985]. Wood anatomy and classification of the Myrtales. Ann. Missouri Bot. Gard. 71: 783–800.

——, J. KOEK-NOORMAN & B. J. H. TER WELLE. 1981. Wood anatomy, classification and phylogeny of the Melastomataceae. Blumea 27: 463–473.